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SUBMISSIVE PANT–GRUNT GREETING OF FEMALE CHIMPANZEES IN MAHALE MOUNTAINS NATIONAL PARK, TANZANIA

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ABSTRACT One of the unique greeting behaviors of chimpanzees (*Pan troglodytes*) is pant–grunt vocalization, which is given only by lower-ranking individuals toward a more dominant group member. It is a typical social behavior performed when adult females encounter adult males. Previous studies have proposed some social functions of pant–grunts, such as signaling submission, signaling appeasement, expressing support, and checking tolerance. To evaluate the social variables driving pant–grunts, I investigated pant–grunts by adult female chimpanzees of the M group in Mahale Mountains National Park, Tanzania. I found that pant–grunts functioned as a submissive signal between adult males and females, but did not always occur during encounters of adult females with adult males. Whether the pant–grunt functions as an appeasement signal remains unclear, but adult females performed pant–grunts as a reaction to the aggression of other individuals. Adult females did not express their support for a particular male by pant–grunting during the study period, probably because the dominance rank among adult males was stable. Rather than checking tolerance at the time, maintaining relations with adult males by pant–grunting was more essential for adult females. Whether adult females performed pant–grunts during encounters with adult males depended on the individuals present, the social power balance, and the current social interactions.

Key Words: Chimpanzee; Pant–grunt; Male–female interactions; Appeasement; Dominance rank; Mahale Mountains National Park.

INTRODUCTION

“Greeting” behaviors play an important role in forming a social unit of chimpanzees (*Pan troglodytes*) because chimpanzees form a fission–fusion society; i.e., group members of both sexes associate in temporary parties that vary in size, composition, and duration (Goodall, 1968, 1986; Nishida, 1968, 1970). Some ritualized gestures and vocalizations by chimpanzees are thought to function to reestablish an immediate status recognition between individuals when they meet after some time of separation (Goodall, 1968; Bygott, 1979). One of the remarkable greetings of chimpanzees is “pant–grunt” vocalization (Marler & Tenaza, 1977; “bobbing pants,” Goodall, 1968; “rapid ohoh,” van Hooff, 1973), which is given only by lower-ranking individuals toward a more dominant individual (Bygott, 1979; Noë et al., 1980). Although it is not controversial whether the pant–grunt is a “submissive greeting” (de Waal, 1982), social variables driving pant–grunt vocalizations are not well understood. For example, when encountering a higher-ranking individual, chimpanzees do not always perform pant–grunts (Hayaki, 1990; Takahata, 1990). Also, pant–grunts usually occur between pairs whose dominance

relations are already apparent due to the difference in body size and other agonistic interactions (Hayaki et al., 1989). These observations suggest that the social function of pant-grunts is more complex than only the expression of subordination or submission.

Previous studies have proposed some social functions of pant-grunts. First, pant-grunts often occur in a moment of tension or excitement, sometimes as a response to an aggressive display. In such cases, pant-grunts may restrain or deflect aggression of dominant individuals, suggesting the function of an appeasement signal (Goodall, 1968; Nishida, 1970; Marler & Tenaza, 1977). Second, pant-grunts may function as a token of respect and support (de Waal, 1982; Goodall, 1986). De Waal (1982) reported a case of captive chimpanzees in which the alpha male was deposed, yet received more frequent pant-grunts from adult females and immature individuals than did the new alpha male for two years. During this period, some females supported the former alpha male against the new alpha male, but none supported the new against the old. In this case, pant-grunts may have been an expression of support for a preferred male. Third, according to a study on pant-grunts of young chimpanzees (Hayaki, 1990), pant-grunts that are performed vigorously seem to signify excitement; moreover, such pant-grunts seem to excite dominant males. In such cases, young individuals may perform pant-grunts to make their presence recognized by the receiver and to check how tolerant the individual is at the time (Hayaki, 1990). Overall, these observations suggest that motives triggering pant-grunts are changeable according to the level of social excitement at the moment, fluctuation of the alpha male, and sex-age classes of performers.

In this study, to evaluate which social variables drive female chimpanzees to perform pant-grunts, I investigated pant-grunt interactions of the M-group chimpanzees in Mahale Mountains National Park, Tanzania. I focused on adult females because they are formally subordinate to all adult males (Hayaki et al., 1989; Hayaki, 1990; Takahata, 1990). In addition, females in estrus more often range together with adult males than do females in anestrus, whereas females in anestrus and noncycling resident females with small, clinging infants do not always remain near adult males when they encounter them (Wrangham, 1979; Takahata, 1990; Matsumoto-Oda, 1999). For anestrus or noncycling resident females, pant-grunts are typical behaviors when encountering adult males (Takahata, 1990; Sakamaki, 2009).

Social functions of pant-grunts proposed in previous studies, i.e., signaling submission, signaling appeasement, expressing support, and checking tolerance, are not mutually exclusive. Therefore, concerning the possibility that pant-grunts are submissive signals, I first examined the directions and frequencies of pant-grunts between adult males and females in relation to the rank order of adult males. I also examined the effects of the alpha male on pant-grunts during encounters, as the alpha male has a prominent and influential status in a chimpanzee society (de Waal, 1982; Hayaki et al., 1989; Kawanaka, 1989). Second, concerning the possibility that pant-grunts are appeasement signals, I examined the effects of aggression by adult males during encounters. Third, I examined pant-grunts by adult females who showed support for a particular adult male. Fourth, to evaluate the motive among pant-grunters to check the tolerance of the receiver,

I compared aggressiveness and bobbing gestures, the features of pant-grunts by immature individuals, among performers from different age-sex classes while pant-grunting (Hiraiwa-Hasegawa, 1989; Hayaki, 1990). From these results, I discuss social variables driving pant-grunts by adult females.

METHODS

I. Study Site and Animals

The study subjects were chimpanzees of the M group in Mahale Mountains National Park, Tanzania. This group has been studied since 1965, and all individuals of the group have been identified (Nishida, 1990; Nishida et al., 2003). Observations were made between October 1999 and September 2000. During this time, the group consisted of 49 to 52 individuals, including eight adult males (16 years of age or older) and 20 adult females (13 years of age or older; see Nishida et al., 2003 for age and sex classes). Individuals were assigned a two-letter identification code. Although the youngest adult male (CT) was estimated to be 14 to 15 years old during the study period, he was categorized as an adult because he had reached adult body size and received pant-grunts from many adult females. Dominance rank among adult males was determined based on the direction of submissive/aggressive behaviors (e.g., pant-grunts, charges, and attacks; Sakamaki, 2005). The group included was one alpha male (FN), three high-ranking males (DG, DE, AL), and four low-ranking males (MA, HB, BB, CT). The alpha status of FN was stable during the study period. Each high-ranking male received pant-grunts from low-ranking males, except in one ambiguous pair (DE/HB).

II. Data Collection

Each day, I followed one individual within visible range as long as possible. When I lost that individual, I followed another one or more individuals to continue observation. The total observation time was 1,261 h, 9 min over 178 days. In total, I followed six adult males (DE, MA, FN, DG, BB, AL) and six adult females (FT, OP, JN, MJ, AB, TZ). Table 1 lists adult males in the M group and the six focal females with focal observation times. My samples were representative of the adult males and females because focal males were chosen from every dominance rank and focal females were chosen from among both older and younger adults in the group.

During observations, I continuously recorded the social behaviors and activities of the focal individual and other individuals near him/her and within sight. To observe them while they traveled on the ground and when they moved quickly, observations were recorded as spoken accounts on a microcassette tape recorder. For analyses of social interactions during encounters and the associations between focal females and adult males (described below), I used the observation data of six focal females, a total of 349 h, 17 min over 47 days, not including observations on days when focal females were in estrus. Other focal observation times

Table 1. Adult males in the M group and six focal females with focal observation times.

Name	Age ^a	Focal days (n)	Focal observation time	Dominance rank
Adult male				
FN	21?	14	109h19m	Alpha
DG	18?	9	64h21m	High
DE	36?	9	70h32m	High
AL	17	8	63h37m	High
MA	22	9	75h42m	Low
HB	19?		(Not a focal individual)	Low
BB	18	8	59h58m	Low
CT	14?		(Not a focal individual)	Low
Name	Age ^a	Focal days (n)	Focal observation time ^b	Offspring ^c ; cycling/no-cycling
Focal female				
FT	36?	10	76h54m	M (11), F (0); no-cycling.
OP	28?	10	76h14m	F (13), M (8), M (1); no-cycling.
JN	25?	7	44h22m	F (4), F (0, born in May 2000); cycling until January 2000.
MJ	19?	8	62h01m	M (3); no-cycling.
AB	17	8	55h25m	F (1); no-cycling.
TZ	17	4	34h21m	No offspring; cycling.

^a Ages at the beginning of 2000. Ages with “?” are estimated.

^b Observations when focal females were not in estrus.

^c Offspring in the M group during the study period. M and F represent male and female, respectively. The numbers in parentheses indicate offspring ages.

when two focal females (JN, TZ) were in estrus were 26 h, 57 min over 3 days and 27 h, 53 min over 3 days, respectively, both of which were part of the total observation time.

III. Data Analyses and Terminology

Because pant–grunt vocalizations may grade into other sounds, such as pants, pant–barks, and pant–screams (Marler & Tenaza, 1977; Hayaki, 1990), the pant–grunt greeting (PGG) was defined as any pant-related sound (i.e., pant, pant–grunt, pant–bark, or pant–scream) toward another individual within 10 m. Pants while playing with other individuals were not included in the definition of the PGG. A performer of a PGG usually approached or was approached by receivers and directed the vocalizations while facing them. Although the performer did not actually come close to receivers who showed aggressive displays, I could easily identify the intended receivers who were within 10 m of the performer.

To calculate frequencies of the PGG when a focal female was associated with adult males, an association was defined as two or more individuals within sight of each other, which included any individual(s) within my sight while I followed a focal individual. I divided continuous focal observations into 10-min observation units (OUs) and expressed the time of association as the number of OUs. While I was following a focal individual, if another individual came into my sight at

least once during one OU, then I counted the association between them as one OU. I used this method because chimpanzees sometimes traveled in low-visibility, thick bushes, and it was difficult to record the distance between individuals and the exact time when individuals appeared within my sight and disappeared out of my sight. The frequency of a PGG by a focal female A toward an adult male B, Freq.PGG.A-B , was calculated as:

$$\text{Freq.PGG.A-B} = \text{No.PGG.A-B} / \text{No.OU.assoc.A-B},$$

where No.PGG.A-B was the number of PGGs that a focal female A performed toward an adult male B, and No.OU.assoc.A-B was the number of OUs of association between a focal female A and an adult male B during the focal observation of A.

Chimpanzees split into small parties to varying degrees, and each individual was not always in visual contact with others even when they traveled roughly in the same direction. Hayaki (1990) defined new encounters as those that occurred after 1 min of separation, and Bauer (1979) defined new encounters (“reunions”) as those that occurred after 30 or 60 min of separation. To exclude repeated encounters after a brief separation, I adopted the definition of a new encounter as one that occurred after 30 min of separation, i.e., when an adult male who had not been associated with a focal female for 30 min or more appeared within sight of a focal female, as judged by my sight. When the next encounter with other adult males occurred within 1 minute of the last encounter, these encounters were treated as one encounter for the analyses.

Concerning the encounters when focal females had previously associated with adult male(s), 75 cases were collected. In 15 of the 75 cases, the adult male(s) who were associated with the focal females had gone out of sight after an encounter and then reappeared later with new adult male comers(s). In such cases, the distinction between encountered males and associated males was ambiguous. Therefore, these 15 encounters were excluded from the analyses of encounters.

In describing my observations, I use the term “charging display,” which comprises nonvocal and vocal displays, the latter of which is accompanied by a pant-hoot, a long-distance call (Nishida et al., 1999). When I analyzed aggression of adult males during encounters, I examined whether they attacked others, directly charged at others, or showed nonvocal displays.

For statistical tests, null hypotheses were rejected at an alpha level of 5% (significance at $P < 0.01$ is also presented).

RESULTS

I. PGG between Adult Males and Females

Concerning the possibility that pant-grunts are submissive signals, I first examined the directions of PGGs between adult males and females. The results showed that adult females always performed PGGs toward adult males, but not vice versa,

Table 2. All pant-grunt greetings (PGGs) performed by adult females toward adult males in the total observation. Numbers without parentheses indicate the number of PGGs directed toward one adult male. Numbers in parentheses indicate the number of PGGs directed toward two or more adult males who were nearby at the time. For each of the latter type of PGG, one PGG was credited to each target adult male. Individuals with an asterisk were focal individuals.

Performer adult females	Receiver adult males								Total
	FN*	DG*	DE*	AL*	MA*	HB	BB*	CT	
CA	39	4	3	2	0	2	3	0	53 (0)
WX	38 (1)	13 (1)	7 (2)	1	1	0	4	1	65 (4)
GW	121 (3)	25	18 (2)	25	1 (1)	2	1	6	199 (6)
FT*	108 (8)	25	39 (10)	31 (3)	18 (1)	6	8	5 (2)	240 (24)
IK	67 (2)	3 (1)	10 (3)	2	5	1	0	0	88 (6)
NK	58 (4)	8 (2)	24 (2)	4	0 (1)	0	0	0	94 (9)
OP*	99 (4)	21	33 (3)	25	13 (1)	6 (1)	6 (1)	5	208 (10)
PI	41 (4)	9 (1)	15 (3)	11	6 (1)	0 (1)	0	2	84 (10)
JN*	31 (3)	8	22 (3)	12	3	3	2	1	82 (6)
XT	105 (3)	11	13 (4)	12 (1)	2	1	1	0	145 (8)
LD	94 (2)	12	7 (2)	11	1 (1)	0	1 (1)	1	127 (6)
MJ*	45 (3)	14 (1)	29 (3)	24 (1)	8	9	8	7	144 (8)
AK	64 (1)	6	13 (1)	11	7	3	2	0	106 (2)
CY	112 (5)	11 (2)	29 (5)	11	5	1	2	1	172 (12)
AB*	40	13	16	15	5	4	0	5	98 (0)
TZ*	131 (7)	6	35 (7)	28	10	2	3	0	215 (14)
RB	85 (4)	9	12 (3)	9	2 (1)	1	1	0	119 (8)
SY	41	16	6	5	3	1	1	2	75 (0)
EF	18 (2)	5 (1)	2 (1)	5 (1)	2 (1)	1	0	1 (1)	34 (7)
ZL	13 (2)	0 (1)	1 (1)	3	6 (1)	1	3	0	27 (5)
Total	1350 (58)	219 (10)	334 (55)	247 (6)	98 (9)	44 (2)	46 (2)	37 (3)	2880 (145)

with only one exception, when an adult male, BB, performed a PGG toward an adult female, CY. Table 2 shows the numbers of PGGs performed by adult females toward adult males during all observations. A total of 2880 PGGs were performed by adult females toward one adult male at a time (numbers without parentheses in Table 2). Another 72 PGGs were performed by an adult females toward two or more adult males who were close to them simultaneously (numbers in parentheses in Table 2; the total number in parentheses is 145 because these were calculated by crediting one PGG to each target adult male). One adult male pair, FN and DE, most often received this type of PGG while traveling on the ground or staying close together, and sometimes while showing charging displays together (48 out of 72 PGGs were performed toward this pair).

Next, with respect to the rank order among adult males, the alpha male (FN) received the most PGGs from adult females (47%=1350/2880). In addition, high-ranking males (DG, DE, AL) received more PGGs (8% to 12%) than did low-ranking males (MA, HB, BB, CT) (1.3% to 3.4%) (Kendall's rank correlation test, $\tau=0.82$, $P<0.05$). Fewer opportunities were available to observe PGGs toward two particular adult males (HB, CT) than toward the other adult males because these two males

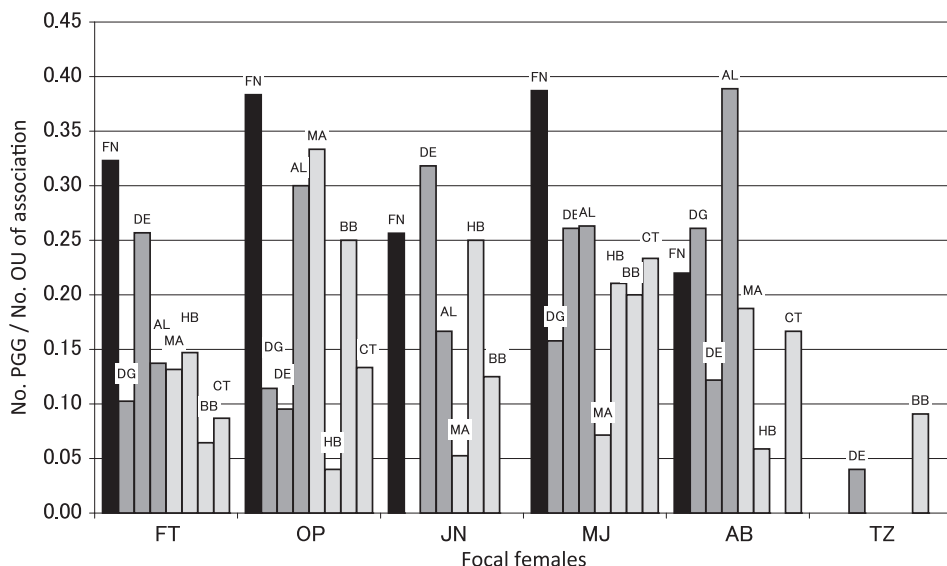


Fig. 1. Frequency of pant-grunt greetings (PGGs) performed by six focal females (FT, OP, JN, MJ, AB, TZ) toward adult males in the M group per 10-min observation unit (OU) of association in each pair.

were not focal individuals (no asterisk in Table 2). On the other hand, the frequencies of PGG, i.e., the number of PGGs per OU of association between each pair of focal females and adult males, did not correspond to rank order among adult males (Fig. 1; Kendall's rank correlation test, each focal female, not significant).

II. Effects of the Alpha Male During Encounters

Here, I show the results of analyses about social interactions during encounters. In total, I observed 231 encounters of focal females in anestrus with adult males. During the encounters, focal females performed PGGs toward adult males in 30% of encounters.

As for the effects of the alpha male, I first examined whether focal females performed PGGs more often when they encountered the alpha male than when they encountered the other adult males. Table 3 compares encounters between focal females and one or more adult males, including the alpha male ($N=58$), with encounters between focal females and only non-alpha male(s) ($N=173$). Five females (FT, OP, JN, MJ, AB) performed PGGs more often when the alpha male was present than when he was not. When focal females performed PGGs toward one or more males, the alpha male was always included if he was present. Overall, females performed PGGs in 48% of encounters that involved the alpha male and in 24% of encounters involving only non-alpha males; the difference was significant ($df=1$, $\chi^2=12.52$, $P<0.01$).

Second, I examined whether the presence of the alpha male affected focal females' PGGs. Table 4 compares encounters with non-alpha males when focal females had previously been associated with the alpha male ($N=34$) with such

Table 3. Instances of pant–grunt greetings (PGGs) performed by focal females while encountering the alpha male (with or without other males present) vs. non-alpha male(s) only.

Encounter with one or more adult males	PGG performed by focal females	Total	Focal female					
	Occurred : Not occurred		FT	OP	JN	MJ	AB	TZ
Including the alpha male	28 : 30	58	10:11	7:3	3:4	4:3	4:8	0:1
Including only non-alpha male(s)	41 : 132	173	9:43	4:18	4:15	12:14	11:28	1:14
Total	69 : 162	231	19:54	11:21	7:19	16:17	15:36	1:15

($df=1$, $\chi^2=12.52$, $P<0.01$)

Table 4. The effects of the presence of the alpha male on pant–grunt greetings (PGGs) by focal females (previously associated with vs. not associated with the alpha male) while encountering non-alpha male(s).

Focal female	PGG performed by focal females	Total	Focal female					
	Occurred : Not occurred		FT	OP	JN	MJ	AB	TZ
Associated with the alpha male	1 : 33	34	1:18	0:6	0:6	0:0	0:2	0:1
Not associated with the alpha male	40 : 99	139	8:25	4:12	4:9	12:14	11:26	1:13
Total	41 : 132	173	9:43	4:18	4:15	12:14	11:28	1:14

($df=1$, $\chi^2=10.08$, $P<0.01$)

Table 5. The effects of the presence of non-alpha male(s) on pant–grunt greetings (PGGs) by focal females (previously associated vs. not associated with non-alpha males) while encountering the alpha male.

Focal female	PGG performed by focal females	Total	Focal female					
	Occurred : Not occurred		FT	OP	JN	MJ	AB	TZ
Associated with non-alpha male(s)	5 : 7	12	2:3	1:1	0:1	1:0	1:2	0:0
Not associated with non-alpha male(s)	23 : 23	46	8:8	6:2	3:3	3:3	3:6	0:1
Total	28 : 30	58	10:11	7:3	3:4	4:3	4:8	0:1

($df=1$, $\chi^2=0.26$, n.s.)

encounters when they had not ($N=139$). When focal females had previously been associated with the alpha male, they performed PGGs when they encountered non-alpha males in only 3% of encounters, whereas when they had not been associated with the alpha male, they performed PGGs in 29% of encounters; the difference was significant ($df=1$, $\chi^2=10.08$, $P<0.01$).

In contrast, previous association with non-alpha male(s) did not affect whether

focal females performed PGGs toward the alpha male. Table 5 compares encounters with the alpha male when focal females had previously been associated with non-alpha males (N=12) with such encounters when they had not been associated with any adult males (N=46). In the former case, focal females performed PGGs toward the alpha male in 42% of encounters, and in the latter case, they did so in 50% of encounters; the difference was not significant ($df=1$, $\chi^2=0.26$, n.s.).

III. Effects of Aggression During Encounters

Concerning the possibility that pant–grunts are appeasement signals, I examined PGGs by focal females or other individuals and aggression of adult males during encounters when focal females had not previously been associated with any adult males (N=171). When adult males showed aggression during such encounters (N=31), PGGs occurred in 84% of encounters; on the other hand, when adult males did not show aggression during these encounters (N=140), PGGs occurred in 40% of encounters; the difference was significant ($df=1$, $\chi^2=19.6$, $P<0.01$). Table 6 shows details of these encounters. In 60 encounters, focal females or other individuals performed PGGs spontaneously toward adult male(s); i.e., adult males did not show aggression when they came in sight. In 93% of encounters, adult male(s) did not spontaneously show aggression. In 25 encounters, adult male(s) showed aggression when they came in sight. In 80% of these encounters, focal females or other individuals performed PGGs at that point. In two encounters, both PGGs by focal females or other individuals and aggression of adult males started simultaneously with adult males coming in sight.

PGGs and aggression during encounters that occurred when focal females had previously been associated with adult males were more complex. I present three such cases.

Case 1 (December 15, 1999; focal individual was FT)

A focal female, FT, was feeding on fruits in a tree. She had previously been associated with two adult males, FN and HB. At 7:37, FN started showing a charging display, i.e., climbing woody vines vigorously and stamping the trunk

Table 6. Pant–grunt greetings (PGGs) of focal females (FFs; not associated with any adult males) and other individuals and aggression of adult males (AMs) when FFs encountered one or more AM.

FF and/or other individuals performed PGG spontaneously;*	60
AM did not show aggression.	56
AM showed aggression then.	4
AM showed aggression when appearing in the sight of FF;	25
FF and/or other individuals performed PGG then.*	20
FF and other individuals did not perform PGG.	5
PGG of FF and aggression of AM started simultaneously.*	2
PGG or aggression did not occur.	84
Total	171

* In these 82 cases in which PGGs occurred, FFs performed PGGs in 62 cases and the other individuals did so in only 20 cases.

of a tree. One individual (unidentified because of low visibility) approached FN and performed a PGG up to a 2-m distance from FN. Then, at 7:38, two adult males, AL and DE, arrived with hair erect. AL stamped rocks and DE threw rocks. Another adult male, MA, also appeared with hair erect. During this time, FT stayed in the tree.

In this case, a focal female (FT) encountered three adult males (AL, DE, MA) but did not have any direct interactions with them. The only obvious social behaviors were the charging displays of the adult males. The focal female seemed not to have a chance to perform PGGs toward the adult males due to the risk of being injured as a result of their aggression. Alternatively, the focal female might not have needed to greet them because the adult males were concentrating on their social interactions with one another.

Case 2 (April 19, 2000; focal individual was AB)

A focal female, AB, and some others were in trees. AB had previously been associated with two adult males, MA and HB. At 14:53, one adult male, FN, arrived showing a charging display. One adult female, EF, climbed a tree while screaming loudly. FN stopped 4 m high in a tree. One juvenile male, PR, approached FN while performing a PGG. FN charged directly at one adult female, TZ (other individuals were also near her in a tree), and then charged at another adult female, AK. FN then climbed down, slapped the ground, and the charging display stopped. At 14:54, AK approached and faced FN while performing a PGG for 23 s. During this time, AB stayed in a tree and did not receive any aggression.

In this case, a focal female (AB) encountered one adult male (FN), but she did not have any direct interactions with him. Because other individuals interacted with FN in an excited condition, AB seemed not to have had a chance, or the necessity, to approach and greet him at that time. In fact, about 3 min later, AB performed a PGG while approaching FN, who was being groomed by an adult male (HB) at the time, and then started grooming with FN.

Case 3 (November 5, 1999; focal individual was OP)

At 14:46, a focal female, OP, started walking on the ground with some individuals including two adult males, DE and BB (OP had previously become associated with them). At 14:47, when DE was passing close to OP, OP performed a PGG toward DE. Then, DE started showing a charging display. At the time, one adult male, MA, arrived with hair erect, and then another adult male, FN, appeared showing a charging display. (At the same time, another adult male, HB, also came into sight.) At 14:48, DE ran away while screaming with a grin. OP, her juvenile son (OR), and her adult daughter (RB) performed PGGs toward FN and MA, who were showing charging displays.

In this case, a focal female (OP) encountered three adult males (FN, MA, HB). Because OP had previously been associated with two adult males (DE, BB), this was probably an encounter among adult males as well. OP first performed a PGG toward DE just before DE showed a charging display. Then, when FN and MA appeared showing charging displays, DE ran away screaming. OP and others performed PGGs toward FN and MA. In this case, the charging displays of FN

and MA seemed to drive OP and others to perform PGGs toward them, but not toward DE, due to their powerful displays.

IV. Support of Adult Females for Adult Males

During the study period, I observed three cases of support of adult females for a particular adult male. In all three cases, one adult male, DG, first charged at or showed a charging display toward another adult male, DE. In the first case, two adult females, NK and PI, chased DG (DE also chased after them), and DG fled; in the second case, PI and another individual(s) (unidentified because of low visibility) chased DG, and DG fled; and in the third case, DE and two adult females, GW and PI, chased DG, and DG fled. The three females, NK, PI, and GW, were not with their clinging infants.

Because these three females were not focal individuals, I calculated the frequencies of PGGs between NK/PI/GW and DG/DE per OU of association in each pair from the data of focal observations of DG and DE. The results indicated that DG received more PGGs than did DE (NK: 0.086, 0.053; PI: 0.286, 0.086; GW: 0.500, 0.034, respectively). During the total observation (Table 2), DE received more PGGs from adult females than did DG (334 vs. 219); NK and PI performed more PGGs toward DE than toward DG (24 vs. 8, and 15 vs. 9, respectively), and GW performed more PGGs toward DG than toward DE (25 vs. 18).

V. Aggressiveness and Persistence by Performer During PGG

Immature chimpanzees may show aggressiveness and bobbing gestures while performing PGGs, perhaps because they intend to make their presence recognized by the receiver and check the tolerance of the individual (Hiraiwa-Hasegawa, 1989; Hayaki, 1990). Here, I compared aggressiveness and bobbing gestures by performers while performing PGGs among different age–sex classes. The number without parentheses in Table 7 shows the number of PGGs in which the performer

Table 7. The number of pant–grunt greetings (PGGs) in which the performers showed aggressive behavioral elements (see text for details). Numbers in parentheses are the number of PGGs in which the performers showed bobbing.

Performer		Receiver						Total
		Male			Female			
		Adult	Adolescent	Juvenile	Adult	Adolescent	Juvenile	
Male	Adult	0	0	0	0	0	0	0
	Adolescent	4	0	0	0	0	0	4
	Juvenile	9 (7)	0	0	0	0	0	9 (7)
Female	Adult	2 (1)	0	0	0 (1)	0	0	2 (2)
	Adolescent	7 (2)	0	0	1	0	0	8 (2)
	Juvenile	1	0	0	0	0	0	1
Total		23 (10)	0	0	1 (1)	0	0	24 (11)

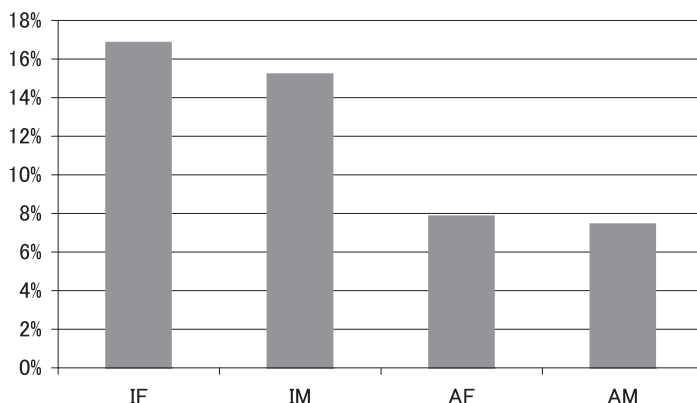


Fig. 2. Percent of aggressive reactions by adult males when receiving spontaneous pant-grunt greetings (PGGs) from immature females (IF, N=101), immature males (IM, N=559), adult females (AF, N=2447), and adult males (AM, N=511).

showed aggressive behavioral elements during the total observation time. In these cases, I observed aggressive behavioral elements that the performers showed during PGGs as follows: shaking/swaying/swinging woody vegetation, throwing branches, stamping on the ground/tree, slapping the ground, and climbing up or jumping down vigorously. The numbers in parentheses in Table 7 show the number of PGGs in which the performer showed a bobbing gesture while performing a PGG. The result indicates that immature individuals more often showed aggressive elements and bobbing gestures while performing PGGs than did adult females, as the total number of PGGs by adult females (N=2447) was higher than those of immature males (N=559) and females (N=101).

On the other hand, adult females also showed PGG performances as follows.

Case 4 (November 11, 1999; focal individual was FN)

The alpha male, FN, was traveling on the ground. At 14:29, an adult female, LD, performing a PGG while approaching FN (emitting pant-grunts that graded into pant-barks). At one point, LD brought her face close to FN's face, then kept walking backward in front of FN. LD again brought her face close to FN's face and jumped back, then kept walking backward in front of FN. Another adult female, XT, also approached while emitting pant-grunts from behind. LD stopped vocalizing and walked ahead of FN (the first PGG from LD lasted for 30 s). LD again looked back to FN while emitting pant-grunts and kept walking backward in front of FN. LD extended her left hand and touched the back of FN. At 14:30, a juvenile male, XM (son of XT), came between FN and LD and then immediately went away. LD stopped vocalizing (the second PGG from LD lasted for 14 s). XT approached FN while emitting pant-grunts. FN kept walking without looking at XT. LD again emitted pant-grunts in front of FN and put her left arm around FN's back. FN passed by LD, and LD grasped FN's back by both hands and walked while mounting ("mount-walking," van Hooff, 1973) (the third PGG from LD lasted for 8 s).

Next, I examined the reactions of adult males receiving spontaneous PGGs

(i.e., PGGs without prior charging displays from receivers). Fig. 2 shows the rate of aggressive reactions of adult males while receiving spontaneous PGGs. Overall, immature females and males received more aggressive reactions (17% and 15%, respectively) than did adult females and males (7.8% and 7.4%, respectively).

DISCUSSION

Chimpanzees have a unique “greeting” behavior, the pant–grunt vocalization, which plays an important role in coexistence in a fission–fusion society, especially for adult females living with adult males (Goodall, 1968; Nishida, 1968; Takahata, 1990). Previous studies have proposed some social functions of pant–grunts, i.e., signaling submissiveness, signaling appeasement, expressing support, and checking tolerance (Goodall, 1968; Marler & Tenaza, 1977; de Waal, 1982; Hayaki, 1990). However, social variables driving pant–grunts are not well understood. To evaluate the social variables driving pant–grunts by adult females, this study investigated pant–grunt interactions in wild chimpanzees.

The submissive-signal social function was supported by this study in that the direction of pant–grunts was almost always from adult females to males, and not vice versa. Although pant–grunts were not observed in some combinations, e.g., between adult females and low-ranking males, a pant–grunt by an adult male toward an adult female was observed only once. As reported in previous studies (Hayaki et al., 1989; Hayaki, 1990; Takahata, 1990), adult females were formally subordinate to all adult males in this study group during the study period, and pant–grunts were available as the typical index used to measure formal dominance between adult males and females.

Second, concerning pant–grunts as an appeasement signal, it is still unclear whether adult females succeeded in restraining or deflecting aggression of adult males by pant–grunting. When focal females (not associated with any adult males) or other individuals performed pant–grunts during encounters with adult males who were not engaged in aggression, the adult males did not show aggression in 93% of the encounters. These observations, however, do not necessarily indicate that the pant–grunts restrained the adult males’ aggression, because it is unlikely that the adult males had previous aggressive intentions in all the cases. It was difficult to judge whether the adult males previously had an aggressive intention when they came within sight. On the other hand, when adult males showed aggression while appearing in sight, focal females or other individuals performed pant–grunts toward the adult males in 80% of encounters. These pant–grunts seemed to occur as a reaction to the aggression. In some situations, chimpanzees participate in social excitement with many individuals, during which noisy displays including pant–hoots, barks, charging displays, and submissive vocalizations are continuously occurring (Nishida, 1970; Goodall, 1986; Sakamaki, 2009). Although to what extent pant–grunts restrain the aggressive intentions of adult males is still unclear, encountering aggressive displays by adult males is likely to trigger pant–grunts by adult females. Additionally, an exchange of aggressive displays and submissive vocalizations could lead to a “mass excitement” situation (Nishida,

1970) involving both males and females.

Third, clear evidence with regard to whether pant-grunts are an expression of support for a particular male was not found in this study. Three cases of support for a particular male by adult females were observed during the study period. However, the supported male did not receive more pant-grunts than did the rival male. This study might not have provided suitable conditions to evaluate this hypothesis because dominance relations among adult males, especially the alpha male status, were stable during the study period (Sakamaki, 2005). Under such stable conditions of dominance relations among adult males, agonistic confrontations among adult males would rarely occur. In a previous study suggesting the merits of the hypothesis that PGGs express support (de Waal, 1982), observations were made during and after the tenure of the former alpha male. To evaluate this hypothesis, a further study during a stage of fluctuation in the alpha status is needed.

Fourth, the hypothesis that the function of PGG is checking tolerance was proposed from the observations of young individuals' pant-grunts, which seemed persistent enough to potentially lead to aggression from adult males (Hayaki, 1990). From the comparisons among different age-sex classes in the present study, aggressiveness and bobbing gestures of performers while pant-grunting appeared to be a characteristic specific to immature individuals, and were not observed among adult females. On the other hand, Case 4 indicated that adult females may also show persistence while performing pant-grunts. However, even when pant-grunts of adult females were persistent, differences between adult females and immature individuals were apparent. First, adult females did not show the same aggressive behavioral elements as did immature individuals during pant-grunting. Second, adult females received less aggressive reactions than did immature individuals while performing pant-grunts toward adult males. When an adult female performed persistent pant-grunts in Case 4, the adult male did not show conspicuous reactions and, on the contrary, seemed to control his reaction. These differences suggest that it is more important for immature individuals than for adult females to make their presence recognized by the receiver of pant-grunts and to determine the tolerance of the individual at the time. For adult females in anestrus who do not always remain near adult males when they encounter them (Takahata, 1990; Sakamaki, 2009), a lasting pant-grunt interaction might in itself, at least sometimes, be important to maintain relations with adult males.

In this study, because I focused on encounters, I discuss pant-grunts as "greetings," which is defined as social interactions between individuals when they meet each other after some separation (Goodall, 1968). This point is still controversial, because adult females performed pant-grunts in only 30% of encounters (defined as individuals appearing within sight after a 30-min or longer separation in this study). In previous studies, for example, Laporte and Zuberbühler (2010) showed that 16% of encounters (defined as individuals entering a 10-m radius) led to pant-grunts; Hayaki (1990) showed that 41% of pant-grunts occurred during encounters (defined as individuals entering a 10-m radius after a 1-min separation), and other pant-grunts did not occur during encounters (although it is noteworthy that the targets of age-sex classes were different in these studies). Although the effect of duration of separation between individuals on greeting behaviors is an unsolved

question, I here discuss some reasons for encounters without pant–grunts.

One of the most important results of this study is the finding that individuals present in the situation affected the performance of pant–grunts. First, the alpha male was not only the target who received the most pant–grunts from adult females, but he also had an influence on pant–grunts toward the other adult males; when anestrus females had previously been associated with the alpha male, if they encountered other adult males, the females rarely performed pant–grunts toward them. Case 3 is noteworthy with regard to the influence of the alpha male because the case suggests that powerful displays by the alpha male drove others to perform pant–grunts toward him. Second, as seen in Cases 1 and 2, even if anestrus females encountered adult males, when other individuals interacted with each other, they did not always enter into the interactions occurring at the time. These observations indicate that anestrus females changed the way pant–grunts were performed according to the individuals present and the social interactions occurring at the time. Such flexible responses of chimpanzees according to the situation might be possible due to their recognition of social complexity.

In conclusion, pant–grunt vocal behavior, known as a “submissive greeting,” functions as a submissive signal, but does not always occur in the “greeting” context because other social variables are related to the performance of pant–grunts. The role of the pant–grunt as an appeasement signal is still unclear, but pant–grunts may occur as a reaction to the aggression of other individuals. Whether adult females express their support for a particular individual probably depends on the stability of dominance rank among adult males. Immature individuals might perform pant–grunts to check how tolerant the receiver is at the time, but for adult females, a pant–grunt interaction may itself be important to maintain relations with adult males in a fission–fusion society. When confronting adult males, adult females make decisions about whether to perform pant–grunts according to the individuals present in the situation and the current social power balance among them.

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